or individual trait complexes reflects biological and behavioral adaptations, while the latter assumes that anatomical changes in specific parts of the body result from shifts in overall body form. We posit that the hand morphology implicated in the evolution of precision manipulation in humans conforms with Churchill's (1996:559) observation of "a high degree of tolerance for particulate evolution in the context of an integrated upper body plan." Marzke's (1997) eight anatomical traits of tool manufacture and use include some that probably were part of the integration of the upper limb for locomotion just prior to the advent of bipedality, some that directly enable the controlled flaking of stone, and some that evolved over time in a particulate response to the benefits of efficient precision gripping.

We promote the study of precision manipulation in a context broader than the question of whether or not a particular hominid species could have made tools or via a narrow focus on the biomechanics of tool use. As a target goal for studies of the evolution of manipulation these approaches inflate the significance of threshold traits and deflate the significance of preadaptations, respectively. Marzke's (1997) study has advanced the comparative anatomy of manipulation to a level that now requires interpretive rooting in integrative rather than particulate evolution. The evolution of precision manipulation is the story of bipedalism, relaxed selection on upper limb joint stability, and the exploitation of progressive efficiency in the application of a preadapted biobehavioral grasping complex.

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Reply

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Hartwig and Doneski imply an evolutionary scenario in which an ancestral hand, specialized for quadrupedal locomotion but preadapted for precision manipulation, does not begin precisely manipulating objects until it is released from locomotor duties by the origin of bipedality. At the time of release, precision manipulation by the earliest bipedal hominids exploits some of the locomotor features compatible with precision manipulation of tools, which are later supplemented by additional features favorable to tool manipulation.

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They contrast this scenario with their own revision of Marzke (1997), in which her so-called "complete package of traits, . . . the minimum combination necessary to initiate efficient manufacture and use of tools," is imposed at one point in time upon an ancestral hand that has been freed from locomotion but lacks facility for precision manipulation.

Contrary to statements by Hartwig and Doneski, the eight traits to which they refer were not presented in Marzke (1997) as having appeared together, nor were they described as a complete package or as a minimum combination necessary to initiate efficient manufacture and use of tools. In fact, 1) their possible sequential order of appearance in the record was traced in the section of the paper on fossil evidence for stages in the evolution of precision grip capabilities and tool behaviors, and 2) the combination of traits was recommended for

use in discerning tool-making capabilities in fossils, a recommendation that should not be mistaken for a suggestion that the combination was a minimum one necessary to initiate efficient manufacture and use of tools. Moreover, it was shown in the sections on chimpanzees and hamadryas baboons that these primates manipulate objects with precision grips whose effectiveness appears to be enhanced by several morphological features distinctive of each species. Precision gripping began long before the origin of hominids.

My own view is that the hands of hominid ancestors were not preadapted in their morphological complexes to the types of human precision manipulation that facilitate many types of early hominid tool manufacture and use. Nor were they specialized exclusively for locomotion. In the course of human evolution, the patterns of hand morphology changed, and were compatible with a succession of combined locomotor and manipulative demands, just as the chimpanzee and hamadryas baboon patterns now facilitate their respective combined locomotor and manipulative roles. The earlier functional complexes of hominid ancestors are no longer intact. However, some elements of earlier complexes persisted because they functioned effectively in newer morphological contexts compatible with changing hominid locomotor, foraging, food-processing, tool-using and tool-making behaviors. As Gebo (1996) noted in his paper cited by Hartwig and Doneski, Marzke has identified some traits in the modern human hand that may have been elements of functional complexes previously associated with locomotor demands. Some of these traits are also consistent with tool manipulation (Marzke, 1971).

With regard to bipedality, I refer Hartwig and Doneski to Marzke et al. (1988) and Marzke (1996), in which the sequential evolution of traits associated with bipedality was specifically addressed. Some traits in the locomotor apparatus of early hominids (together with a pattern of traits in the hand) form a functional complex that in our view is consistent with possible use of the trunk as leverage for enhancing tool use in bipedal *posture*. Additional traits of the lower limb apparatus appeared later in human evolution, some of them perhaps in connection with bipedal striding *locomotion*.

Further on the subject of locomotion, it is not clear how the "integration of the upper limb for locomotion," to which Hartwig and Doneski attribute some (unidentified) anatomical traits of tool manufacture, relates to the concept they draw from Churchill (1996) of an integrated upper body plan, which Churchill attributes to genetic and morphological constraints. It appears that they are trying to distinguish a functional complex of traits that facilitated locomotion from other functional complexes that were compatible with, and in some cases evolved in adaptation to manipulation. This is a different distinction from one between traits constrained by their integration with overall body form and traits with fewer constraints on their evolutionary change. The concept is clouded further in the last paragraph of their comments, in which the integrative approach now seems to be one that simply incorporates both locomotor and manipulative traits in the analysis of hominid hand evolution.

If Hartwig and Doneski mean by "threshold traits" autapomorphic traits for humans, and by "preadaptations" primitive traits shared with apes, they are correct that we need to understand how all these traits function together in the hands of modern humans and other primates. This has been the focus of our combined electromyographic and kinematic studies (Marzke et al., 1998; Marzke et al., in review). It should also be noted that our approach reported in Marzke (1997) has been anything but narrow and restricted to the single question of which hominid species made tools, and that it is founded on both qualitative and quantitative data derived from modern humans and nonhuman primates, and not exclusively from anatomically modern humans as Hartwig and Doneski state.

Only the initial steps have been taken in identifying elements that make up the successive ancestral patterns of hominid hands, and in designing experiments with which to discern the functions and potential biological roles of these patterns. It is hoped that Marzke's (1997) conclusions from the review

of the current state of the field will serve as a catalyst for more extensive, quantitative studies of the eight traits discussed in the paper and for the collection and analysis of three-dimensional quantitative data on bone and joint morphology associated with muscle attachment areas and tendon moment arms. We are encouraged that Hartwig and Doneski share our concern, which generated the paper (Marzke, 1997), that debates about human hand evolution must escape the narrow confines of single traits, a single precision grip, and the single manipulative activity of tool making.

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